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RESEARCH ARTICLE

Quantifying the attractiveness of broad-spectrum street lights to aerial nocturnal insects

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Abstract

1. Sodium street lights, dominated by long wavelengths of light, are being replaced by broad-spectrum, white lights globally, in particular light-emitting diodes (LEDs). These white lights typically require less energy to operate and are therefore considered “eco-friendly”. However, little attention has been paid to the impacts white lights may have upon local wildlife populations.
2. We compared insect attraction to orange (high-pressure sodium, HPS) and white (metal halide, MH and LED) street lights experimentally using portable street lights and custom-made flight intercept traps.
3. Significantly more (greater than five times as many) insects were attracted to white MH street lights than white (4,250 K) LED and HPS lights. There was no statistical difference in the numbers of insects attracted to LED and HPS lights for most taxa caught. However, rarefaction shows a greater diversity of insects caught at LED than HPS lights.
4. *Policy implications.* With the current, large-scale conversion to white light-emitting diode (LED) lighting, our results give insight into how changes to street light technology may affect wildlife populations and communities. We recommend avoiding metal halide light installations as they attract many more insects than competing technologies. We highlight the need to tailor LED lighting to prevent disturbances across multiple insect taxa.

KEYWORDS

artificial light, Coleoptera, Diptera, high-pressure sodium lights, LED, Lepidoptera, light pollution, metal halide lights, nocturnal insects, street lights

1 | INTRODUCTION

Street light technology has changed radically over the last century (Fouquet & Pearson, 2006). Incandescent and mercury vapour street lights used during the first half of the 20th century were gradually superseded by low-pressure sodium (LPS) and high-pressure sodium (HPS) lighting technologies. More recently, sodium street lights have begun to be replaced by metal halide (MH) lights and by energy-saving, light-emitting diodes (LEDs). Both technologies typically emit broad-spectrum, white light, although their emission spectra usually differ. One main difference is that LEDs typically do

not emit ultraviolet (UV) light, whereas MH bulbs do (Figure 1). The attraction of insects to UV light is well documented (Barghini & de Medeiros, 2012; Eisenbeis, 2006; Shimoda & Honda, 2013; Worth & Muller, 1979) and so it is likely that the two lighting technologies will differ with regard to the impact they have on insect ecology and behaviour. While investigating insect attraction to street lights at a single site adjacent to the river Rhine in Germany, Eisenbeis and Eick (2011) found that traps on LED and MH street lights caught an average of 12.1 and 50.9 insects per trap night respectively. They concluded that LEDs appear to be “very insect friendly” (Eisenbeis & Eick, 2011).

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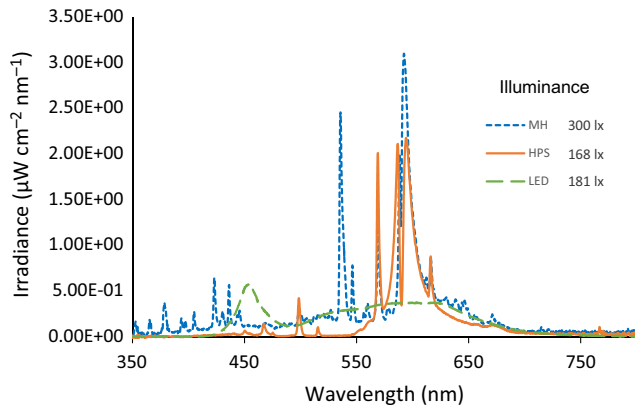


FIGURE 1 Irradiance and illuminance measures of the three street lights used in this study: high-pressure sodium (HPS), light-emitting diode (LED) and metal halide (MH). Irradiance readings for each street light were taken in a darkened room using a cosine corrector at the end of a 400 μm diameter, ultraviolet–visible, fibre optic cable connected to a spectrometer (USB2000; Ocean Optics, Dunedin, FL, USA) controlled by a PC running SpectraSuite (version 6; Ocean Optics). Each curve represents the average of three scans. Illuminance readings were taken using a digital lux meter (1330, TES Electrical Electronic Corp., Taipei, Taiwan). All measurements were taken 170 cm directly below each light [Colour figure can be viewed at wileyonlinelibrary.com]

Following the recent global financial recession, many local authorities have suffered monetary cut-backs and are looking to use their resources more efficiently. Authorities are also required to reduce carbon emissions in line with national and international legislation. Energy-saving, “eco-friendly” street light technologies are being adopted world-wide, with large areas being switched from orange/yellow sodium lights (long-wavelength dominated) to white (broad-spectrum) lighting. Switchovers can happen relatively quickly, e.g. in the UK, Cornwall County Council (CCC) planned to replace c. 47,000 sodium street lights with MH in just 3 years as part of their “Invest-to-Save” project (Williams, 2009).

With large-scale installations happening so rapidly, it is important to know how changes in street lighting technology may affect wildlife. Stone, Wakefield, Harris, and Jones (2015), working in conjunction with CCCs “Invest-to-Save” project, found that activity of common pipistrelles, *Pipistrellus pipistrellus*, increased around MH lights following the switchover from LPS lights. As these bats hunt insects around lights (Rydell, 2006), and many insects are disproportionately attracted to UV light (Barghini & de Medeiros, 2012), this higher bat activity is likely to be a result of higher prey abundance at UV-emitting, broad-spectrum MH lights. Relative to sodium lights, white lighting is predicted to: increase the bandwidth of wavelengths to which species are visually sensitive; alter species interactions (Davies, Bennie, Inger, Hempel de Ibarra, & Gaston, 2013); and to “exacerbate ecological impacts” of street lights (Pawson & Bader, 2014).

We compared the relative attractiveness of three common street light technologies (HPS, LED and MH) to volant insects. We tested two hypotheses:

1. MH street lights attract more insects than LED and HPS lighting.

2. Broad-spectrum “white” lights (MH and LED) attract a greater diversity of insects than long-wavelength-dominated (HPS) street lights.

2 | MATERIALS AND METHODS

2.1 | Study sites

Experiments were carried out at 12 field sites across southern England between 3 July and 10 September 2014. Sites were located an average of 115 km apart (range 1–256 km) to: (1) maximise the diversity of insects caught; (2) reduce any potential impact of the experiment on local insect populations; and (3) generate a clearer picture of how street lights are affecting insect attraction over a wide spatial scale (see Figure S1). Sites consisted of linear woodland edges ($n = 10$) or hedgerows ($n = 2$) at least 170 m in length, which adjoined either open meadows or grazed pasture. Woodland edges and hedgerows were selected for the study because they are linear features along which street lighting is often found in suburban areas and along minor roads in semi-rural and rural areas. Each site was sampled for one night and located >100 m from existing artificial lighting to minimise the impact of existing lighting.

2.2 | Lighting equipment

Three different street light technologies were tested: HPS (50 W SON-T, 4,400 lm; Philips, Amsterdam, The Netherlands); LED (2×8 LED Axia module arrays, 3,200 lm, 4,250 K; Urbis Schröder, Basingstoke, UK); and MH (45 W CPO-T, 4,750 lm; Philips). All lights were suitable for installation at a height of 5 m along minor roads or in suburban settings. These lights are deemed to be of similar light output for human needs and therefore are likely to be found on the same types of roads and in similar habitats. It is important to note that these lights vary in intensity as well as their spectral characteristics (Figure 1). Our goal was to measure relative insect attraction to three commercially available lighting technologies, and so it was not necessary to match lights for absolute intensity. However, lights were housed in matching luminaires (Sapphire 1; Urbis Schröder, Chineham, Basingstoke, Hampshire, UK) to control for any potential differences in insect attraction caused by different housing designs. As many existing street lights are being updated by retrofitting of LED or MH units rather than entire luminaire replacement, this is an accurate reflection of current street lighting practice.

Each light, as well as a fourth “control” (CON) light which remained switched off throughout the study, was top-mounted onto a 5-m high tripod (REF 49-Z; Powerdrive Drum Company Ltd, Leighton Buzzard, Bedfordshire, UK) using a custom-made aluminium adaptor. This set-up conforms to the mounting specifications of the lights. The four lighting columns were spaced an average of 34 m apart (range 32–35 m; Figure 2), which is representative of the 35 m distance between actual street lights of this type (Fotios et al., 2012). Lights were powered by a portable generator (Eu10i; Honda (UK), Bracknell, Berkshire, UK), positioned a mean of 97 m away (range = 78–100 m)

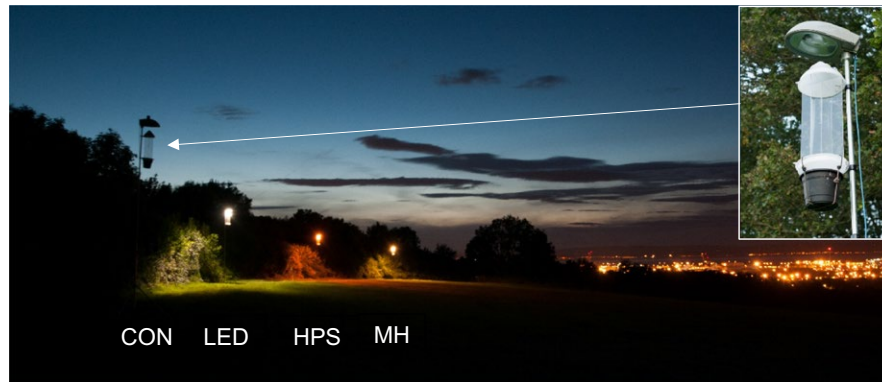


FIGURE 2 A photograph of a typical field site. Main: four street lights are positioned c. 34 m apart along the edge of a hedgerow, approximately uniform in height along its length. The lights were control (CON), light-emitting diode (LED), high-pressure sodium (HPS) and metal halide (MH) and were orientated to illuminate away from the hedge into open grassland. In this example, the positioning of the CON and MH lights were classed as “edge” and the LED and HPS lights as “centre” for the purposes of statistical analyses. Inset: a photograph of one of the custom-made insect flight intercept traps. Traps were designed to channel insects through the lower funnel and into the black collection chamber below. Ethyl acetate in the collection chamber was used to prevent insects escaping [Colour figure can be viewed at wileyonlinelibrary.com]

to minimise the risk that noise from the generator would affect animal behaviour (Stone, Jones, & Harris, 2009, 2012). An electrical splitter was used to enable all experimental lights to be powered from the same generator. The order in which the four luminaires were arranged was randomised between sites and their relative positions, recorded as either “edge” or “centre” (Figure 2), were included in statistical analyses to account for potential edge effects.

One of the lights (HPS) was fitted with an active photocell (SELC 8480; SELC Ireland Limited, Ballycoolin, Dublin, Ireland) designed to turn the light on once ambient light intensity (illuminance) levels dropped below 35 lux. Once this light turned itself on, the other two lights (LED and MH) were manually switched on to ensure that all lights were tested across the same time period. The following morning the photocell would automatically turn the HPS light off once ambient light exceeded 17.5 lux, and then the LED and MH lights were switched off manually. Insect sampling took place on nights with a favourable weather forecast (no rain and wind speed <19 km/hr); actual measurements of humidity, temperature and wind speed were recorded with a portable weather station (Watson W-8681-SOLAR; Flightstore, Pilot Supplies Limited, Mirfield, West Yorkshire, UK) installed halfway between the two central lights.

2.3 | Insect trap design

Insects were caught using custom-made flight intercept traps based on the design used by Eisenbeis and Eick (2011). Flight intercept traps consisted of crossed baffles made from 3-mm-thick Perspex measuring 60 cm in height and 28 cm in width. The Perspex was sandwiched between two 28 cm diameter plastic funnels. The top funnel provided support to the structure and was sealed with tape at the smaller opening to prevent insects flying upwards and out of the trap. The bottom funnel channelled insects into a black plastic collection pot (Figure 2) attached to the bottom funnel using two bungee cords. An open-topped glass vial containing cotton wool soaked in 15 ml of ethyl acetate was placed in each collection pot to detain any insects which

entered the chamber. The top of the plastic baffle was positioned 20 cm below the street light when attaching the traps to the lighting columns. This distance ensured that the trap was close to the light (and therefore to flying insects being attracted to the light) without considerable baffling of the downward-emitted light. The traps were attached to the lighting column and the lights were erected to operational height (5 m) no earlier than 30 min prior to sunset. This allowed sufficient time for all of the equipment to be set up before the lights were switched on, but reduced the time available during which diurnal insects could enter the traps by chance.

2.4 | Insect collection and identification

All traps were dismantled and removed immediately after the lights were switched off each morning. Samples were labelled, then frozen or preserved in ethanol (>70%) for identification at a later date. The majority of insects were identified to family level. Many of the commoner insects were also identified to genus and species. Samples were identified using Unwin (1981, 1984, 2001), Elliot and Humpesch (1983), Chinery (1993), Roberts (1995), Plant (1997), Watson and Dallwitz (2003), Oosterbroek (2006), Luff (2007), Waring, Townsend, Tunmore, and Lewington (2009), Barnard and Ross (2012) and Sterling, Parsons, and Lewington (2012).

2.5 | Statistical analyses

To test whether MH street lights attract more insects than HPS and LED lights, data were analysed by fitting generalised linear mixed models (GLMMs) with Poisson error structures using the package lme4 (Bates, Maechler, Bolker, & Walker, 2014) in R (version 3.4.0. 2017). “Light” was included as the sole fixed effect term and “light position” (“edge” or “centre,” e.g. Figure 2) nested within “site” was included as a random effect in each GLMM. Response variables included “total number of insects,” “Diptera,” “Coleoptera,” “Lepidoptera,” “Erebidae,” “Chironomidae,” “Noctuidae” and “Psychodidae.” Catches of other

taxa were too small for reliable statistical analyses. The goodness-of-fit of each GLMM was tested using the R package *aods3* (Lesnoff & Lancelot, 2013) to ensure data were not overdispersed (residual deviance > degrees of freedom; Crawley, 2008). Each model was then compared to a subsequent model lacking the fixed effect term “light” to examine both the Δ deviance between the corresponding models as well as the difference in Akaike information criterion (AIC) values (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Pairwise comparisons between the different light types were then conducted using Tukey contrasts via the R package *multcomp* (Hothorn, Bretz, & Westfall, 2008).

Rarefaction curves were generated to compare insect diversity at all light types. Both sample-based (incidence data) and individual-based (abundance data) rarefaction and extrapolation curves were created using the iNEXT online program (Chao, Ma, & Hsieh, 2016).

3 | RESULTS

Data from 12 sites were included in the following analyses. The use of the photocell resulted in the lights switching on an average of 15 min

after sunset (range = 4–23) and switching off a mean of 22 min before sunrise (range = 9–30), giving an average sampling duration of 498 min (range = 416–626). The spiders (Araneae, $n = 6$), mites (Acari, $n = 119$) and springtails (Symphypleona, $n = 4$) caught in the flight intercept traps were not included in the analyses. Moon illumination ranged from 6% to 100% across all sites (Thorsen, 1995–2017). At the 10 sites where weather variables were successfully recorded, we recorded an average humidity per night of 92% (range 81%–97%), nightly temperature of 13°C (range 9–17°C) and nightly wind speed of 0.8 km/hr (range 0–2.6 km/hr).

3.1 | MH street lights attract more insects than HPS and LED lighting

In total 1,382 insects were caught: 469 Diptera, 406 Coleoptera, 381 Lepidoptera, 75 Hemiptera, 19 Hymenoptera, 12 Psocoptera, 8 Neuroptera, 5 Ephemeroptera, 5 Tricoptera and 2 Thysanoptera. The CON, HPS, LED and MH light traps caught approximately 1%, 10%, 14% and 75% of insects respectively. On average 115 insects (range = 44–436) were caught per site, with a mean of 1 for CON (range = 0–3), 11 for HPS (range = 3–30), 16 for LED (range = 6–44)

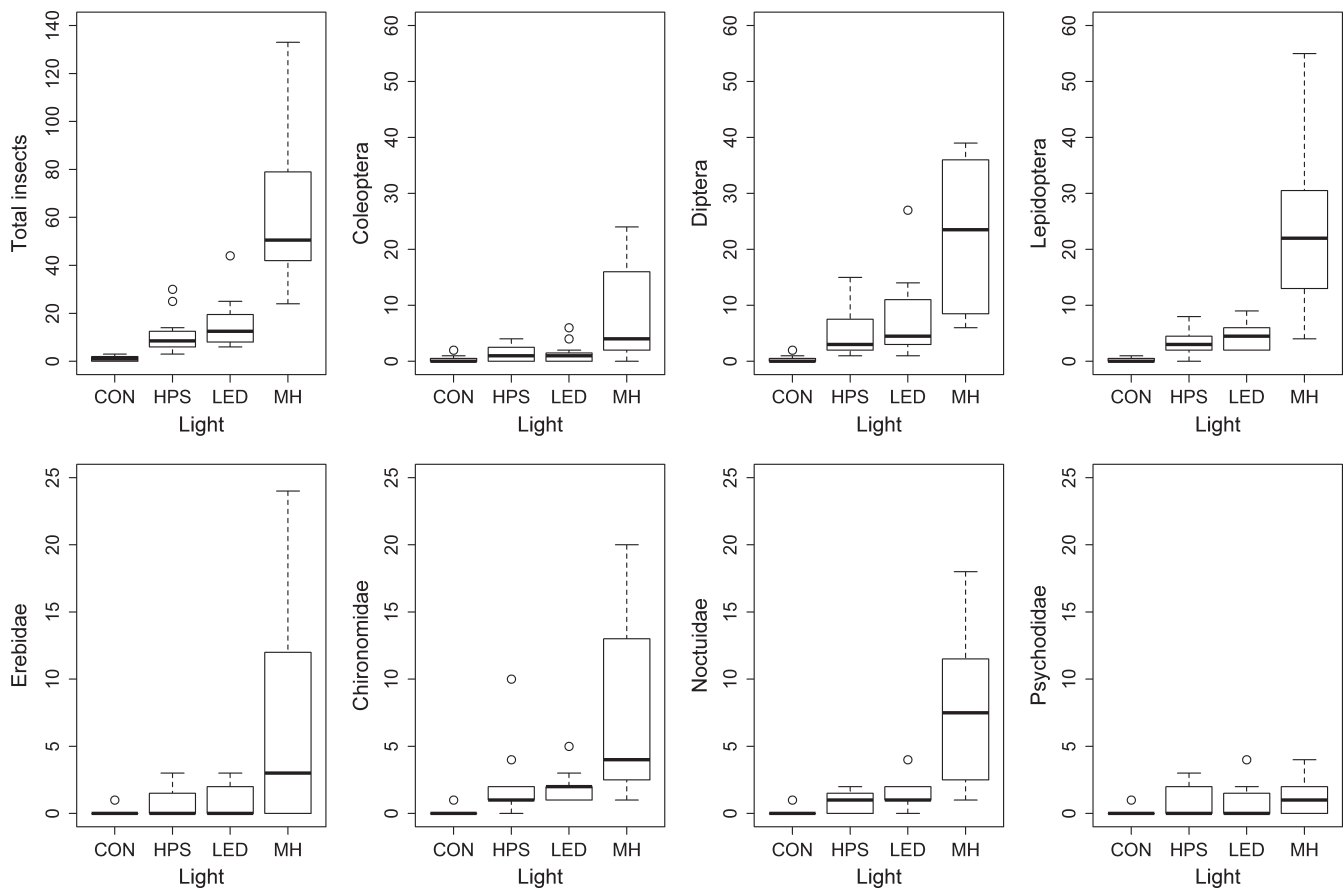


FIGURE 3 Tukey boxplots showing the 25th and 75th percentiles and median number of insect taxa caught per light type: control (CON); high-pressure sodium (HPS); light-emitting diode (LED); and metal halide (MH), for all 12 sites. Circles denote outlying data points where relatively large numbers of insects were caught at some sites

and 87 insects per site for MH (range = 24–407). Median values for total insects caught per light are shown in Figure 3. Total insect attraction was significantly affected by light treatment (Table 1). Pairwise comparisons show the MH attracted significantly more insects than all other lights, but there was no significant difference in insect attraction between LED and HPS lights. All lights caught a greater number of total insects than CON (Table 2).

Total Coleoptera, Diptera, Lepidoptera, Erebidae, Chironomidae, Noctuidae and Psychodidae were all significantly affected by light treatment (Table 1). The MH light attracted significantly more Coleoptera, Diptera, Lepidoptera, Erebidae, Chironomidae and Noctuidae than CON, HPS and LED lights. The MH light attracted significantly more Psychodidae than the CON and LED but not the HPS light. Coleoptera was the only taxon with a statistical difference in the number of insects attracted between HPS and LED lights; the HPS caught significantly more beetles than the LED light (Table 2 and Figure 3).

3.2 | Broad-spectrum, “white” lights (LED and MH) attract a greater diversity of insects than long-wavelength-dominated (HPS) street lights

The number of insect orders caught varied with light type; CON = 4, HPS = 8, LED = 8, MH = 10. In total 1,372 insects were identified to family; 10 could not be positively identified beyond order (eight Lepidoptera and two Ephemeroptera) and were therefore omitted from family-level analyses. Abundance data are displayed by family in Table S1.

Sample-based rarefaction curves indicate family diversity was greatest at the MH, followed by LED and then the HPS light. These differences are significant based on 95% confidence intervals (Figure 4a). However, individual-based rarefaction curves show a higher species

diversity at LED lights compared to HPS and MH lights when rarefied down to the number of individuals observed at the HPS light (Figure 4b). Extrapolations of the HPS and LED data suggest that the curves for these lights may cross with that of the MH at larger sample sizes, although the 95% confidence intervals for these extrapolated data become very large.

4 | DISCUSSION

The MH street lights attracted significantly more insects than LED and HPS street lights, as predicted in our first hypothesis. Analysis of incidence data, which accounts for sample (site) heterogeneity, indicates that broad-spectrum, white lights attract a greater diversity of insects than long-wavelength-dominated (HPS) street lights (hypothesis 2). However, when controlling for the number of individuals caught at each light type, the rarefied family diversity is significantly higher at the LED than at the HPS and MH lights. Regardless of rarefaction method, the LED attracted a greater number of families than the HPS light (Figure 4a,b). However, as rarefaction curves for all lights have not reached a clear asymptote these results should be treated with caution. Insect diversity estimates for each light may alter relative to one another with greater sample size, as suggested by extrapolation of our data.

Light intensity was not equal for all street lights, as we compared lighting technologies based on their real-life application for human needs. However, these differences in intensity are unlikely to have influenced insect attraction as much as spectral differences (Longcore et al., 2015). Despite both emitting white light, the MH caught approximately five times as many insects as the LED light. This may be, in part, explained by the presence of UV light in the MH spectrum and its absence in the HPS and LED spectra (Figure 1). Many insects find

Taxon	Light term	AIC	Deviance	χ^2	df	p
Total insects	Present	1,414.26	1,408.26	1069.1	3	<.001
	Absent	351.13	339.13			
Coleoptera	Present	604.28	598.28	414.03	3	<.001
	Absent	196.24	184.24			
Diptera	Present	584.81	578.81	324.04	3	<.001
	Absent	266.77	254.77			
Lepidoptera	Present	528.44	522.44	316.29	3	<.001
	Absent	218.15	206.15			
Erebidae	Present	208.45	202.45	86.712	3	<.001
	Absent	127.74	115.74			
Chironomidae	Present	269.40	263.40	102.42	3	<.001
	Absent	172.99	160.99			
Noctuidae	Present	252.94	246.94	111.67	3	<.001
	Absent	147.27	135.27			
Psychodidae	Present	182.51	176.51	44.17	3	<.001
	Absent	144.34	132.34			

TABLE 1 Results of comparisons between identical generalised linear mixed models differing only in the inclusion of the single fixed term “light”

TABLE 2 Results of multiple comparison tests using Tukey corrections applied to GLMMs for insect catches (12 sites). In all models, “light position” nested within “site” was included as a random effect term and “light” as the only fixed effect term. Lights were control (CON), high-pressure sodium (HPS), light-emitting diode (LED) and metal halide (MH)

	Estimate	SE	Z value	p
Total insects				
HPS-CON	2.215	0.297	7.460	<.001*
LED-CON	2.230	0.290	7.678	<.001*
MH-CON	4.404	0.295	14.939	<.001*
LED-HPS	0.014	0.131	0.108	1.000
MH-HPS	2.189	0.136	16.079	<.001*
MH-LED	2.175	0.114	19.038	<.001*
Coleoptera				
HPS-CON	1.256	0.600	2.094	.144
LED-CON	0.229	0.596	0.384	.979
MH-CON	3.429	0.566	6.062	<.001*
LED-HPS	-1.027	0.403	-2.547	.048*
MH-HPS	2.172	0.370	5.874	<.001*
MH-LED	3.200	0.265	12.072	<.001*
Diptera				
HPS-CON	2.495	0.515	4.848	<.001*
LED-CON	2.738	0.511	5.357	<.001*
MH-CON	4.585	0.520	8.819	<.001*
LED-HPS	0.242	0.191	1.270	.558
MH-HPS	2.089	0.212	9.879	<.001*
MH-LED	1.847	0.179	10.315	<.001*
Lepidoptera				
HPS-CON	2.590	0.595	4.354	<.001*
LED-CON	2.890	0.590	4.903	<.001*
MH-CON	4.550	0.577	7.889	<.001*
LED-HPS	0.300	0.207	1.447	.433
MH-HPS	1.960	0.168	11.678	<.001*
MH-LED	1.660	0.148	11.251	<.001*
Erebidae				
HPS-CON	2.080	1.061	1.961	.180
LED-CON	2.398	1.044	2.296	.185
MH-CON	4.344	1.006	4.316	<.001*
LED-HPS	0.318	0.465	0.685	.891
MH-HPS	2.264	0.372	6.096	<.001*
MH-LED	1.946	0.322	6.037	<.001*
Chironomidae				
HPS-CON	3.238	1.004	3.226	.005*
LED-CON	3.119	1.010	3.089	.008*
MH-CON	4.559	0.994	4.585	<.001*
LED-HPS	-0.119	0.315	-0.376	.979
MH-HPS	1.321	0.265	4.985	<.001*
MH-LED	1.440	0.251	5.728	<.001*

(Continues)

TABLE 2 (Continued)

	Estimate	SE	Z value	p
Noctuidae				
HPS-CON	2.303	1.033	2.230	.098
LED-CON	2.773	1.015	2.732	.026*
MH-CON	4.511	0.990	4.556	<.001*
LED-HPS	0.470	0.397	1.184	.604
MH-HPS	2.208	0.328	6.732	<.001*
MH-LED	1.738	0.267	6.512	<.001*
Psychodidae				
HPS-CON	2.201	1.103	1.994	.174
LED-CON	1.287	1.087	1.183	.618
MH-CON	3.297	1.073	3.072	.010*
LED-HPS	-0.914	0.517	-1.766	.270
MH-HPS	1.097	0.483	2.270	.095
MH-LED	2.010	0.417	4.817	<.001*

*A significant ($p < .05$) difference.

short wavelengths of light highly attractive (Eisenbeis & Hänel, 2009; Van Langevelde, Ettema, Donners, WallisDeVries, & Groenendijk, 2011) and the presence of UV light, even in small quantities, is a disproportionate lure to insects (Barghini & de Medeiros, 2012). Many invertebrates have eyes capable of detecting UV light and have evolved to use it beneficially for navigation, foraging and mate choice (Tovée, 1995). However, if UV, or wavelengths of light adjacent to UV, disrupt natural behaviour by enticing insects towards artificial lighting, then survival and reproduction may be negatively affected (Frank, 2006). Even *reductions* in flight-to-light behaviour of urban moths, predicted to increase survival and reproduction, may reduce moth mobility, with subsequent negative connotations for foraging, colonisation and pollination (Altermatt & Ebert, 2016). Disruption of ecosystem services, such as pollination by Lepidoptera (see Macgregor, Pocock, Fox, & Evans, 2015), is likely to induce trophic cascades and may have implications for human food security.

All lights were mounted at the same height within the same luminaire model, yet there were still differences in the spatial distribution of the emitted light. Qualitatively, the HPS and MH (both gas discharge) lights had similar, diffuse, light distributions, whereas the light from the LED (solid state lighting) appeared to focus light in two distinct planes (Figure 2). Given that flying insects can approach the vicinity of a street light from any direction, the downward-focused LEDs should, on average, be less visible than those which shine light both downwards and at higher elevations. Consequently, the difference in insect attraction between the LED and MH lights may be, in part, due to a difference in the spatial distribution of emitted light. Full shielding of lights has been recommended to limit the impact of light pollution on the environment (Falchi, Cinzano, Elvidge, Keith, & Haim, 2011), but we suggest that further quantitative study investigating how light distribution impacts taxa would have useful policy implications.

Degen et al. (2016) have estimated an attraction radius of 23 m for moths at HPS lights. This suggests that for our light separation distance

of 34 m (typical for UK street lights), there will be overlap of attraction radii for moths. We chose to compare lights together as ratios of moths caught at spectrally different lights have been found to be consistent regardless of whether the lights were presented “alone” or in “competition” with one another (Somers-Yeates, Hodgson, McGregor, Spalding, & French-Constant, 2013). Testing in “competition” allowed us to control for environmental variables, but it should be noted that, generally, different types of street lights are not mixed.

Excluding Coleoptera, there was no statistically significant difference in the number of insects caught at HPS and LED street lights. Experiments conducted in New Zealand (Pawson & Bader, 2014) found that LEDs attracted 48% more insects than HPS street lights, whereas a study in Germany (Eisenbeis & Eick, 2011) found that LEDs attract significantly fewer insects than HPS. LEDs can vary considerably, with high “correlated colour temperature” (CCT) rated LEDs emitting relatively more blue light than low CCT LEDs. The LED light we used was rated as “neutral white” at 4,250 K, slightly “cooler/bluer” than the 4,000 K LEDs used by Pawson and Bader (2014). Differences in CCTs are unlikely to be the main cause of disparity here as abundances of insects caught at LEDs varying in CCT did not differ from one another statistically (Pawson & Bader, 2014; Wakefield, Broyles, Stone, Jones, & Harris, 2016); although see Longcore et al. (2015) concerning LED spectral-tuning. Therefore, we predict that differences in our results are more likely to be the result of variation in habitats surveyed and the associated variation in insect assemblages that were sampled, as well as the aforementioned differences in light distribution between the lights tested.

Analysis of sample-based (incidence) rarefaction curves show significantly more families were caught at the MH relative to the LED light, which itself caught significantly more families than the HPS (comparisons made at $n = 12$ sites, Figure 4a). As insect catches varied considerably between lights, and a larger sample from an assemblage is statistically more likely to contain more families, we also generated individual-based rarefaction curves. These interpolate (and extrapolate) results while standardising catches for abundance. These individual-based curves differ from the sample-based results in all but one relationship—a significantly higher diversity of insect families at LED relative to HPS lights (comparisons made at $n = 136$ individuals in Figure 4b). As these curves, especially those for the HPS and the LED, had not reached a clear asymptote, this indicates that many other families are likely to be sampled at all lights with greater sampling effort.

As a single entity, broad-spectrum white lighting (i.e. LED and MH) did not attract a greater number of insect families relative to long-wavelength-dominated HPS lighting. We highlight that differences may occur at a finer taxonomic resolution which could have implications for conservation work often carried out at the species level. Typically, insect vision is di- or trichromatic, with peak sensitivities at shorter wavelengths including UV (Land & Nilsson, 2012). Sodium lights predominantly emit longer wavelengths (Figure 1) but do still emit light throughout the rest of the visible spectrum and attract more insects than monochromatic long-wavelength lighting, e.g. LPS (Rydell, 1992).

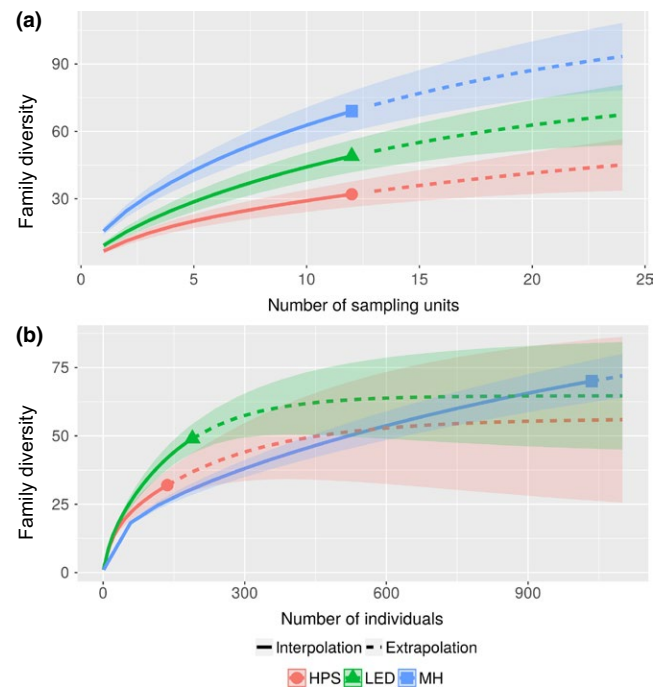


FIGURE 4 Rarefaction curves showing means for interpolated (solid lines) and extrapolated (dashed lines) family diversity as well as 95% confidence intervals (coloured area around each mean) for: (a) sample-based (incidence) data; and (b) individual-based (abundance) data. High-pressure sodium (HPS); light-emitting diode (LED); and metal halide (MH) ($n = 12$ sites for both) [Colour figure can be viewed at wileyonlinelibrary.com]

The MH light caught approximately twice as many families of Coleoptera and Lepidoptera as the LED light, despite both appearing white to the human eye. Similar observations have been made in other studies (Nabli, Bailey, & Necibi, 1999; Somers-Yeates et al., 2013). Differences in visual capabilities between insect species and the complexity of ecological networks make it difficult to predict exactly how changes in lighting spectra will affect insect populations. Effects other than phototaxis, such as disrupting sex pheromone production (Van Geffen et al., 2015), diapause inhibition and sex-specific life-history changes (Van Geffen, van Grunsven, van Ruijven, Berendse, & Veenendaal, 2014), are also dependent on spectral compositions, being most affected by white and green light. Therefore, the use of white lighting may affect a wider range of insects, and other wildlife, via trophic cascades.

Contrary to Coleoptera and Lepidoptera, Diptera were most diverse around the LED light (see Table S1). Flies can be attracted to short wavelengths as well as green and red light (Green, 1985). Differences in the range of visual spectra between insect orders may be the cause of these differing trends. This suggests that different insect orders will be affected to differing extents by future street light installations/conversions. Certain LEDs, particularly those with greater short wavelength emissions, may well exacerbate the ecological consequences of artificial lighting at night (Gaston, Davies, Bennie, & Hopkins, 2012; Van Grunsven et al., 2014), although effects on moth populations have yet to be observed (Spoelstra et al., 2015). Advances in LED efficacy and decreased product costs are likely to result in illumination of

previously unlit areas world-wide. The implications of this for dipteran vectors of disease are discussed by Wakefield et al. (2016).

Our finding that MH street lights attract significantly more flying insects than sodium lights compliments research investigating bat activity around street lights (Stone et al., 2015). It is likely that the higher bat activity recorded by Stone et al. (2015) around MH relative to LPS lights was in response to higher densities of prey around the former. As well as attracting insects and creating local abundances of prey for predators such as bats (Rydell, 2006), white street lights can also interfere with the predator avoidance behaviour of a number of moths, reducing their ability to avoid hunting bats (Svensson & Rydell, 1998; Wakefield, Stone, Jones, & Harris, 2015). The underlying causes of insect attraction to light remain unclear, but spectral changes to street lights will have significant impacts on various taxa, altering species distributions, wildlife communities and predator–prey interactions.

White lighting is not always as “eco-friendly” as advertised and thus energy credentials should not be the sole focus for defining how “eco-friendly” a product is. Greater numbers of insects were attracted to MH street lights and a greater diversity of insects were attracted to white LEDs compared with long-wavelength-dominated HPS lights. Placing these results alongside the existing literature we conclude that whole-scale conversion to broad-spectrum, white, street lights is likely to have negative effects on wildlife. Highly focused/shielded LEDs designed to filter out short wavelengths of light may attract relatively fewer insects and warrant further investigation.

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AUTHORS' CONTRIBUTIONS

A.W. co-designed the study, collected and analysed field data and drafted the manuscript. M.B. collected and analysed field data. E.S. was involved in study design and obtaining funding. S.H. and G.J. were involved with securing funding, study design and co-ordination, and edited the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.27q57> (Wakefield, Broyles, Stone, Harris, & Jones, 2017).

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